RECENT STUDIES OF THE VERTEBRATE HEAD.

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FROM researches on Amphioxus and the Craniata Van Wijhe ('89) concludes that the skull never consists of metameres; that only in the occipital region behind the vagus were there at one time separate cartilaginous neural arches. The parietal musculature, and the peripheral nervous system, with the exception of the I., II., and III. nerves, were once segmented in the region of the head, as well as in the body. The number of the myotomes of the head is in general nine, but in those Craniata which have no hypoglossus, less. To a cranial or a body segment belong both a dorsal and a ventral nerve, which were originally separate. Wherever in the Craniata the ventral roots are wanting the corresponding myotomes do not appear. The vagus is a complex of two dorsal nerves. There are no grounds for assuming that the Craniata ever possessed more than eight branchial sacks, unless an additional aborted one belongs to the hyoid arch.[1]

Beard ('89*a*) states that certain portions of the cranial and spinal nerves arise not as outgrowths from the central nervous system, but from the ectoderm just outside the neural tube. This mode of development agrees with that described by Kleinenberg for the parapodial ganglia of Annelida. The parapodial ganglia arise as ectodermal differentiations just above the lateral limit of the ventral cord, and like the ganglia of vertebrates arise segmentally. It is to be noted that Rabl and Dohrn both controvert the above theory. Beard farther says that before the closure of the two limbs of the neural plate the neuro-epithelium of one limb is separated from that of the other by a ciliated groove. Two bands of neuro-epithelium separated by a ciliated groove are characteristic of Annelids. This ciliated groove in vertebrates later forms most, if not all, of the ciliated epithelium of the permanent central canal.

[1] It is interesting to compare the above statements of Van Wijhe with the more recent observations of Dohrn.

Beard ('89*b*) reiterates his former conclusions that the nose, like the ear, represents a branchial sense organ. The olfactory nerve, like a typical branchial nerve, develops from two sources: from the ectoderm just outside the foundation of the central nervous system, and from the special neuro-epithelium.[2] The latter grows in length by increase within itself, and later on in development, in many cases it divides up into a number of smell-buds, comparable exactly to the sense organs of the lateral line. The origin of the olfactory nerve in reptiles is essentially similar to that in Elasmobranchs. In the chain connecting the sensory cells of a vertebrate sense organ with the central nervous system there are ganglion cells arising from three different sources: from the neuro-epithelium itself; between the lateral ganglion and the central nervous system; as a special differentiation in the central nervous system. Jacobson's organ is a specially differentiated part of the nose. There is nothing in the development of the nose *per se* to suggest a gill-cleft.

Golowine ('90*a*) confirms many of the statements of Beard. He thinks that in the chick the ectoderm situated at the sides of the not-yet-closed medullary tube represents two sensitive organs, and that from these latter the ganglionic system is developed. Beard had stated that the ganglion Anlagen are, after the first stages, independent of the ectoderm, but Golowine observed their formation from ectoderm cells up to the time the neural ridge is complete. In most respects he agrees with Beard as to the origin of the Anlagen. Before the neural ridge segments it becomes separated from the sensitive ectoderm by a layer of indifferent ectoderm. Thus in the so-called sensitive organ can be recognized two distinct portions: ganglion Anlagen and the Anlagen of the special sense organs. The neural ridge in the cephalic region divides successively into three ganglion groups. Kastschenko's conclusion that the dorsal parietes of the medullary tube degenerates to such an extent that a second closing occurs is erroneous. As the neural ridge divides, to each ganglionic segment corresponds a segment of sensitive ectoderm, which

[2] Beard, it should be remembered, holds that the neural ridge is independent of the central nervous system.

latter is to be regarded as an organ of special sense. The subsequent development of the ganglionic system is entirely independent of the special sense organs. Though later the ganglia in the region of the head are directly connected with the branchial sense organs, yet the former are never developed at the expense of the latter, Beard, Froriep, and Spencer to the contrary. The olfactory ganglia are probably formed from the neural ridge. They are not derived from the cells of the nasal fossa. The posterior roots of the cranial and spinal nerves are at first cellular, and are formed from that part of the neural ridge placed between the dorsal borders of the medullary tube.

Houssay ('90), in his observations on the development of the Axolotl, agrees with Beard as to the ectodermal origin of the Anlagen of the dorsal nerve-roots. The cranial ganglia first appear as an unsegmented ectodermal band, which afterwards extends into the trunk, forming the lateral line and nerve. In the meantime, while this posterior differentiation is occurring, the band anteriorly segments to form the cranial ganglia. The central nervous system, though at first unsegmented, is soon metameric, both in brain and spinal cord, and this metamerism is called "neurotomy." The dorsal nerve-roots arise each behind the "neurotome" of its segment,[3] this relation being secondary. The author thinks there is a complete homodynamy of the peripheral nervous system in all the metameres of the body. In discussing the metamerism of the head he states that the segments do not appear with any regularity as to time and location. The neurotomes, neuromeres, branchiomeres, and myotomes agree in the manner of segmentation. He believes he finds evidence of the existence of an oculohypophysial, a buccal, a hyomandibular, and an auditory segment. The IV. and VI. nerves cannot be certainly identified as ventral roots.

Gaskell ('89*a*, '89*b*, '90) considers the central nervous system of vertebrates as made up of two parts: a non-nervous supporting tube, and a nervous portion surrounding that tube. He bases his observations on Ammocœtes, and concludes that the non-nervous tube is the altered alimentary canal of a Crustacean-like

[3] *Vide* Platt and McClure.

ancestor. The functions of the supraœsophageal and the infrasœophageal ganglia and the ventral chain correspond to the functions of those parts of the vertebrate central nervous system which are situated in the same anatomical position, with respect to the non-nervous tube, as the corresponding ganglia of the Crustacean with respect to the alimentary canal. The Crustacean cephalic stomach is represented in the brain of the Ammocœtes by the choroid plexuses, the continuation of the tissue of the latter that lines the cavities of the brain being the ventral portion of the stomach walls. The nervous masses lying outside this lining epithelium are probably composed of tissue arranged in the same way and of the same structure as the supraœsophageal, infraœsophageal, and thoracic ganglia of the Crustacean-like ancestor. The two nervous masses which form the brain proper and olfactory lobes are in the position of the supraœsophageal ganglia with respect to the walls of the cephalic stomach, and in connection with a special optic portion which gives rise to eyes of a strictly Arthropod type. Rudiments of the old mouth and œsophagus are seen in the infundibular process. A bilaterally arranged mass of pigmented tissue that fills up a large portion of the space around the brain is looked upon as the rudiment of the Crustacean liver, while its duct is seen in the conus postcommissuralis. The pigment is regarded as the remains of the blood channels of the old cephalic liver. The original Crustacean-like ancestor had a pair of median eyes, represented in the Ammocœtes by the " dorsal " and " ventral " pineal eyes, the dorsal eye remaining functional much longer than the ventral. The central nervous system of the Ammocœtes, and therefore of all other vertebrates, is the direct descendant of the Arthropod nervous system in all respects. The vertebrate alimentary canal is formed by the prolongation of a respiratory chamber, the latter containing the gill-bearing legs of the ancestral form; the legs being still present in Ammocœtes in the form of branchial bars. The segmental cranial nerves are the nerves arising from the infraœsophageal and thoracic ganglia. The first two cranial nerves are the nerves of special sense arising from the supraœsophageal ganglia.[4]

[4] To fully comprehend the above theory one must ignore all morphological principles.

Miss Platt ('89) finds that in the chick the first mesodermal cleft occurs anterior to the first protovertebra, and that two protovertebræ are subsequently formed anterior to this cleft. The four pairs of protovertebræ entering into the formation of the head are thus evenly divided by the first mesodermal cleft. During the second and third days of incubation the medullary tube becomes divided by a series of constrictions into vescicles or neuromeres. Anterior to the first protovertebra there are seven of these neuromeres. As the protovertebræ are successively formed, neuromeres are added, each opposite a protovertebra; but as the neuromeres often appear before the corresponding protovertebræ, the former are independent of any mechanical influence of the latter. The anterior neuromere gives rise to the prosencephalon, thalamencephalon, and mesencephalon. The development of these three brain vescicles is coincident with the cranial flexure, and the latter may be due to the rapid development of the dorsal and lateral walls of the first cerebral vescicle. From the second neuromere is developed the cerebellum. The succeeding vescicles, including those between the first five protovertebræ, share in the formation of the medulla oblongata. Orr and Béreneck correctly described the number and appearance of the neuromeres, and the ultimate relations of the cranial nerves to these medullary folds observed by them in the lizard and chick are the same as those observed by Platt in the salmon and chick. The primitive relation in the chick is different. The V. nerve arises not as Béreneck says, from the outward convexity of the first neuromere of the medulla, but from the concavity between the first and second neuromeres. Opposite this concavity a ridge[5] projects into the fourth ventricle, composed of lines of cells converging like the rays of a fan toward the point of origin of the V. nerve. At the time when the VII. and VIII. nerves have just left the neural ridge, from the concavities between the second and third and the third and fourth neuromeres spring nerve-fibres which unite in a large ganglion. Thus at an early period the VII. and VIII. nerves are distinct from each other, but as the third neuromere is smaller than the others the space between the roots

[5] See Orr. *Journ. Morph.*, Vol. I., No. 2, p. 335.

of these two nerves is very slight. The IX. nerve arises from the concavity between the fourth and fifth neuromeres. The X. nerve is evidently made up of the fused roots of several spinal nerves. The latter arise like the cranial nerves from corresponding concavities in the spinal cord. The cranial neuromeres are to be regarded as homologous with the neuromeres of the spinal cord. Orr stated that the internal ridges projecting into the fourth ventricle corresponded not to the nerve-roots, but to the spaces between the nerve-roots. In Acanthias, Platt ('90) describes a pair of head-cavities anterior to the premandibular cavities. This observation is of great interest in the light of Dohrn's recent studies on Torpedo.

While many observers have noted the relations of the cranial nerves to the neuromeres, McClure ('89, '90) seems to be the first to attempt to comprehend the entire brain in a schematic, segmental arrangement of neuromeres. Basing his observations on the embryos of Amblystoma, Anolis, and the chick, he concludes that the primitive brain consisted of approximately ten neuromeres, which, beginning with the anterior, he calls olfactory, optic, oculomotor, trochlear, trigeminal, abducens, facial, auditory, glossopharyngeal, and vagus neuromeres respectively. He follows closely the observations of Orr on the lizard, and quotes his definition of a typical neuromere.[6] The forebrain is to be considered as consisting of two neuromeres and possibly part of a third, the midbrain of two, and the hindbrain of six. "The olfactory neuromere is connected with the olfactory nerve." The two neuromeres of the forebrain described by McClure are the same as those described by Orr in the region of the thalamencephalon of the lizard posterior to the secondary forebrain. But Orr says "they never give off any nerves." As McClure studied Orr's preparations, this disagreement is interesting. The segmental nerve belonging to the optic neuromere is assumed to have degenerated. The midbrain probably consists of two neuromeres, since the III. and IV. nerves arise from this brain segment, and the view is further strengthened by the fact that Scott figures in Petromyzon an appearance of neuromeres in the midbrain.

[6] Orr. *Journ. Morph.*, Vol. I., No. 2, p. 335.

Hoffmann found that the trochlear nerve arises in the lizard from the anterior neuromere of the hindbrain, and subsequently shifts forward to the midbrain. McClure promises to prove that Hoffman has probably mistaken the posterior segment of the midbrain for the anterior segment of the hindbrain, but as he figures in the chick and lizard an unnamed neuromere between the midbrain and trigeminal neuromere, the promise is not fulfilled. This unnamed neuromere is described by Orr. Hoffman says it forms part of the cerebellum. Miss Platt, with whom McClure closely agrees in many points, but whose work he utterly ignores, states essentially the same. Four neuromeres of the hindbrain give rise to dorsal nerve-roots. The abducens and auditory neuromeres possess no nerve-roots, and in Amblystoma the abducens neuromere is wanting. The VI. nerve cannot be certainly identified with any neuromere. It should be noticed that while McClure gives theoretical evidence for the separate origin of the VII. and VIII. nerves, Miss Platt has already demonstrated the same. McClure agrees with Miss Platt in homologizing the neuromeres of the brain with those of the spinal cord. He considers the dorsal roots of the nerves to arise from the outward convexity of the respective neuromeres, or to be intersomitic. Miss Platt says that in the chick the spinal nerves spring from the internal ridge opposite the myotomes or somites. Houssay says that in the Axolotl the dorsal nerve-roots arise each behind the neurotome of its segment. Nine myotomes in the body region would correspond to the nine spaces between ten neuromeres of the spinal cord. Therefore our author says the nine mesodermal head-somites, or myotomes, of Van Wijhe "theoretically correspond to the nine spaces between the ten encephalomeres."[7]

Ayers ('90*a*, '90*b*) sees in Amphioxus, which, as Steiner showed, consists of a series of physiologically equal segments, a region comparable to the brain of higher vertebrates. The anterior end of the neural axis of Amphioxus is a brain, for it terminates the

[7] This statement shows a surprising lack of acquaintance with the morphology of the head. Moreover, Dohrn's recent investigations show conclusively that the primitive brain consisted of many more than ten segments.

neural axis anteriorly; it is intimately connected with the sense organs, eye and nose; it gives off at least two pairs of sensory nerves with peripheral ganglia; it possesses ganglionic centers of coördination; it has an enlarged central canal with three diverticula, two optic and one olfactory; it is the largest part of the nervous system in early stages; it possesses a cranial flexure; it shows a differentiation into ganglionic and fibrous tracts. The large collections of ganglion cells just posterior to the thalamocœle are homologous with the medullary nuclei of other vertebrates. In the ontogeny of other vertebrates the brain passes through a condition which remains as adult in Amphioxus. All the sense organs of the anterior end of the body of Amphioxus are probably paired. The eye-spot is the forerunner of the vertebrate eye, and shows several stages in development. The pigment of the eye-spot is contained in cells that lie normally inside the bounds of the nerve-mass. The pigment bodies form a part of segmental sensory structures. Each of the pigment bodies forms a deposit in an amœboid cell. The pigment of the the axial nervous system of Amphioxus is in process of migration towards the anterior end of the body. The vertebrate ear has developed within the phylum above Amphioxus, and arose from one of the primary sense organs of the lateral line system, at a period phylogenetically later than the formation of the canal system of these sense organs. The ear capsula does not separate two morphologically different portions of the brain.[8] The higher sense organs of all the Cyclostomata are all paired. The parietal-pineal eye of the Cyclostomata and other vertebrates has been developed from a median portion of the pigmented eye of Amphioxus. The neural axis of all vertebrates is coëxtensive with that of the chorda. The pituitary prominence of the skull of vertebrates does not mark a fixed point. The chondro- or ossicranium possesses no more segmental value than the intestine. The head-cavities possess relatively the greatest importance before a primordial cranium has made its appearance. The hypophysis arose in the vertebrate phylum long after the appearance of the chorda, and was connected with the infundibulum. It arose as a

[8]See Rabl. Theorie des Mesoderms.

taste organ, and the infundibulum was its nerve. The optic and trochlear chiasms have arisen within the vertebrate group above the Amphioxus condition. The large number of gill-slits in Amphioxus is due to physiological conditions, the branchial apparatus serving for collecting food as well as for respiration.

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